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ON  
THE DEVELOPMENT  
OF THE  
ORGANIZATION  
IN  
PHÆNOGAMOUS PLANTS.

BY  
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XXVI. *Some Observations on the Development of the Organization in Phænogamous Plants.* By Dr. M. J. SCHLEIDEN.\*

[With a Plate.]

Nulla modo generationem explicasse judicare possum eos, qui ne ullam quidem partem, ne ullum attributum quidem corporis ex traditis suis principiis explicuerunt, sed sermones saltem de ea re fecisse, utcunque doctos, veros et elegantes.

C. F. WOLFF, — *Theoria Generationis*.

ALTHOUGH it must be granted that Linnæus had a tolerably clear idea of the metamorphosis of plants, yet the introduction of this doctrine and its reception into the higher botany takes its date from Goethe. Long, however, before Goethe, the ingenious C. F. Wolff had shown how fruitful this idea could be rendered; but his work was little read by the botanists of the time, not at all understood, and soon forgotten. Thus the science, to its prejudice, did not gain possession of this doctrine through Wolff, in whose hands it would probably have become so fertile, but through Goethe, and owing to the manner in which it was introduced

\* From Wiegmann's *Archiv für Zoologie*, Part IV., Berlin, 1837.

[The Editors are indebted to the kindness of Dr. Wood, of Bristol, for the translation of this paper.]



by him, it has hitherto been of comparatively but little service. If we understand by the term metamorphosis the principle that a plant has only a certain limited number of different fundamental organs, and that all other organs distinguish themselves from these potentially, only inasmuch as the tendency exists in them of allowing a certain peculiar degree of development and variety of form, which, however, is not so absolute but that it can be suppressed under certain circumstances, allowing the usual form of the organ to manifest itself,—I say, if we lay down this principle as a foundation, it is clear that this doctrine must furnish the most important results for the science, and give it an internal unity which no other branch of empirical natural science has hitherto obtained; that is, if this idea can be substantiated by fact; and it must only be received so far as it can be proved, since as much as does not actually exist in nature and cannot be perceived by the senses, is no longer an object of natural science and can never serve to extend our knowledge of the material world.

C. F. Wolff adopted the only correct plan, that of the study of the development, and proved the identity of the greater part of the foliaceous organs quite satisfactorily. He was, however, not at all appreciated, and Goethe was the first who introduced the doctrine of metamorphosis, but not as an induction arising out of practical consideration of the process of development, but as the speculative result of the comparison of the different forms of the developed organ. Now such a comparison may certainly lead us to conjecture the existence of such a law, but can never lead to its absolute establishment. Goethe says in another place:

“ Alle Gestalten sind ähnlich, doch Keine gleicht der Andern;  
Und so deutet der Chor auf ein geheimes Gesetz.”

Analogy pervades all forms,—yet all unlike;  
The whole thus indicate a hidden law.

Thus it was that the botanists received this important doctrine, one which was capable of yielding such valuable results, under a wrong light, since it was presented to them only as a philosophical idea, and indeed it seems as if a tolerably general conviction prevailed that the demonstration of what was true in the theory was not possible. At a later period Francis Bauer, who like Wolff was no botanist, again had recourse to the only correct method, inasmuch as he traced the individual organs to their original forms, in order to explain their proper nature; his investigations have, however, unfortunately become too little known and have been used to advantage by scarcely any one else than Robert Brown.



In this manner has the doctrine of metamorphosis or the morphological design of the organs of plants gradually formed itself into a peculiar department of scientific botany ; and at the same time that it has offered a field for the exertions of the most celebrated men, upon which they have obtained lasting honour, it has become the appropriate theatre for all friends of enigmas, dreamers, and dealers in paradoxes, and has served for the display of the most wonderful things, which have been unhesitatingly dignified with the proud name of Philosophy or Speculation. Speculation, however, is only admissible where our means of observation fail us ; and if it thrusts itself forward, desirous of taking the place of observation, we should do wisely to get rid of it as a tiresome guest. How much might we be in advance of our present position, even in the speculative sciences, were it not that speculation devoted itself to objects, which, consuming its best time and best powers, not only did not require it, but would even have been better without it ! It is precisely in the history of development that examples of this sort are particularly frequent. If therefore the prosecution of this branch of science shall attain importance and become established in all its parts, it will not suffice that investigations be commenced on a bean or something of that sort which may conveniently be dissected with a penknife ; a much earlier period must be chosen, that of the first origin of the embryo. A ripe seed presents the young plant already provided with such manifold organs, that a wide field is here opened to mere speculation sufficiently extensive to render subsequent investigations vague and unprofitable.

Upon its first appearance the embryo is recognised as a membranous cylinder (Pl. III., fig. 9 & 13) rounded and closed superiorly, but open inferiorly, since the membrane constituting the embryo is invariably continued into the sac containing it (appearing indeed to be merely a reduplication of that sac) and filled with an organizable, for the most part pellucid fluid mass, which becomes gradually converted into cells, beginning from above downwards, (fig. 6 & 10) during which process the cellular nuclei also become apparent (fig. 12 & 24), which appear at all times to perform a principal part in the formation of cells. At this point a leading phænomenon in vegetable life finds its explanation. The embryo originally consists of axis alone, and being closed superiorly, only allows a further development from within outwards, but is not limited inferiorly ; and by the secretion of organizable matter becoming transformed into cells, admits of unlimited prolongation ; whence not only the direction but the mode of growth

of the stem and root, differing as they do, become intelligible. During the second stage of the development the upper end of the germ expands in a globular form, (fig. 6, 7, 11, 12, 14, & 15,) and from the sides of this globular extremity, in dicotyledonous plants, the two rudimentary cotyledons become developed as cellular projections, their points being more or less free \* (fig. 16 & 17). In these, as also in the stem itself, the elongated cells and spiral vessels are not formed until a much later period: the mode in which this growth takes place was in its principal features described with perfect accuracy by C. F. Wolff. In the monocotyledonous plants, on the other hand, an asymmetrical elevation is formed at the summit of the cylindrical embryo (fig. 8), which ultimately constitutes the cotyledonous leaf surrounding the stalk, and which also subsequently incloses more or less the terminal bud (*plumula*) †. This process offers the second and greatest difference to which a plant can lay claim, namely, the antagonism between vertical longitudinal formation and horizontal superficial extension.

All subsequent development of the plant, and every later formed organ, are only modifications of these two portions of the axis, the *stem*; and of the lateral organs, the *leaves*. This antagonism therefore appears to be something original; indeed the axis is formed at an *earlier* period than the cotyledons, from which may be seen the great error of that opinion which considers the stem to consist of adherent leafstalks, and the terminal bud to be an axillary one, as for instance Agardh does. The most important points of difference in the cotyledons are again repeated in the leaves also, which are indeed only after-formations of those organs: thus for example we find in the *Stapeliæ*, in

\* *Punctum vegetationis*, according to C. F. Wolff.

† It will be seen from this description of the process of development that every monocotyledonous embryo possessed originally a *plumula exserta*, and that wherever this is inclosed, there must invariably be a fissure present, however fine it may be. The grasses have been usually understood to belong to the families with a *plumula exserta*, but quite incorrectly, since the *plumula* in this family becomes *perfect* by means of an elevation of the cotyledon closed with the exception of a very fine slit (the outer closed leaf of botanists), and this portion of the cotyledon, like every other of its peculiarities, becomes repeated in the subsequent leaves in the analogous formation of the ligula, whilst the *scutellum*, constituting the principal portion of the cotyledon, corresponds to the leaf itself. Sometimes the cotyledon folds itself together once more, as in *Zea Mays*, which formation has been falsely compared to the fissure of the cotyledon in the *Aroidæ*; or it sometimes forms on its anterior surface small protuberances, which however cannot be considered as second cotyledons, since they are in connexion with the axis at a point lower down than the cotyledon itself; and a second leaf cannot possibly be formed beneath the earlier one.



which the cotyledons are very small, that the leaves are also rudimentary, and in *Cuscuta* the absence of the cotyledons in the embryo even points to the subsequent habit of the plant. The close agreement between the cotyledon of grasses and the leaves has already been alluded to in the preceding note.

The investigation of the laws of position of the leaves forms a very interesting section of this inquiry; the manner in which the varying relations of foliage become developed out of the originally opposed and perfectly cotemporaneous cotyledons, until nature often appears to return at the extremity of a plant to the original type of two opposite leaves. The consideration of this subject would however lead me too far beyond the limits of these brief remarks.

It will be unnecessary that I should make any remark as to the calyx and corolla being foliaceous organs, since that is universally received. I will merely remark that in all monopetalous calices and corollæ, those parts which at a later period are joined together, forming the single leaf, are in the earlier stages without exception so independent as to render all discussion as to the number of the individual parts superfluous, since it is a matter of investigation to be established by actual evidence. Every flower then has in its earliest development a regular construction, and the supposed abortions which sometimes appear in the arrangement of the leaves, and which have often been so completely misunderstood, especially whilst the diversity of the laws as to number was disregarded, are therefore entirely unfounded, wherever they cannot be actually proved.

The *Euphorbiæ* have with injustice been denied the benefit of their original structure. Their *involucrum* is not formed out of five leaves, but out of two quintuple verticils, of which the outer one develops the glands; these even exhibit earlier than the five inner leaves a middle nerve with evident spiral vessels, which cannot therefore be considered to be *vasa recurrentia* from the other. There can nowhere be found a better example of the original regularity of structure of the flower than in the grasses, in which the flower becomes at a later period so contorted by unequal development, adhesions, and suppressions of individual parts that every possible explanation has been offered excepting that which nature herself offers. For instance in *Secale cereale*, the *spicula* consists of a lateral *rachis*, on which about five alternating flowers are formed. The superior three of these, together with that portion of the axis which appertains to them, remain in a rudimentary state, whilst on the other hand the two inferior are at first perfectly regular in their development. In the axilla of every bractea (*gluma* auct.) we find a flower consisting of a

calyx of three parts, each leaf of which is completely divided from the others, equally large, and standing at the same height; the two inner leaves become gradually united, and form with the external one, which has grown disproportionately large, the later developed *paleæ* auct. Of course under these circumstances the inner one possesses the two central nerves of the formerly separate leaves. With these parts belonging to the calyx there alternate three corollary leaves (*squamulæ* auct.), forming an inner circle, and in like manner standing at the same height; of these, that which is directed towards the axis becomes at a later period abortive through pressure. We find also further, three stamens *alternating regularly* with these corollary leaves, the two inner of which, although at a later period, are thrust by the lateral pressure towards the side of the ovarium; lastly, the basis of the entire flower, the very short *pedunculus*, cannot, on account of pressure, extend itself horizontally upon the secondary rachis, and is therefore forced to ascend upon the inner side, by which means that part of the flower which is directed towards the *rachis spiculæ* assumes an apparently greater elevation than the outer does. In this manner probably we may be able to explain in a simple manner the apparently complicated development of the flower in the *Gramineæ*.

We will now pass to the consideration of the stamens. These are more deserving of attention, since some (among others Agardh, following Wolff, whom, however, he does not quote, although he is otherwise well acquainted with him,) have appeared disposed to give them the character of buds; the opinions also concerning the formation of the anthers are not yet unanimous.

It is evident likewise from the study of their development that the stamens are modified leaves, for they constantly appear at a *later period* than the petals (although they afterwards develop themselves more rapidly); they stand at first higher up upon the axis than the preceding circle of corollary leaves, and alternate invariably with them; by this means, and from the smallness of the individual parts, the relative proportions can be much easier observed\*, and for this reason they cannot be axillary buds of the calyx.

\* In some families the petals and sepals, (as is frequently the case with the stamens) or indeed other *perigonial parts*, consist of more than one circle of leaves, as, for instance, in the *Berberideæ* of 2-3 leaved, in the *Thymeleæ* of 2-leaved circles; we can here therefore speak of opposition with as little correctness as in the *Liliaceæ*. Whenever actual opposition of the outer circle of stamens towards the inner circle of petals occurs, it will always be found that an intermediate circle of stamens has become abortive.



The incorrectness of Agardh's view is also made evident by a consideration of those flowers, in which the internode between petals and stamens is perfectly developed, as in some *Capparidæ*.

The regularly formed leaf consists of a central rib, on each side of which there is a twofold cellular tissue, between which the nerves take their course. In this manner is the anther naturally formed, whose superior and inferior cellular tissue\* is converted into pollen on both sides of the principal nerve; thus is formed the anther with four cells, which we find to be the general law.

I have found the anther before its bursting quadrilocular in more than one hundred families; amongst these I may name *Gramineæ*, *Cyperaceæ*, *Liliaceæ*, *Labiataæ*, *Borragineæ*, *Scrophularineæ*, *Synanthereæ*, *Umbelliferæ*, *Ranunculaceæ* with its allies, *Rosaceæ* (Juss.), and the *Leguminosæ*, which alone constitute almost one-half of the entire vegetation of the globe. It has been often asserted that the anther could not originally be quadrilocular, since it springs open with two fissures only; that is as much as to consider two chambers as one, because they have not folding doors, but simple doors placed close together. Properly speaking every anther really bursts open with four fissures; they appear however only as two because each pair lies at the sides of the common septum. The difference between quadrilocular and bilocular anthers of descriptive botany, (here however the *Antheræ dimidiatæ* and some few others must be excepted,) consists in this alone: whether the valves detach themselves from the septum earlier or later, in the close observation of which we may distinguish every state of transition.

Sometimes, though rarely, the original middle layer is not developed, and in this case of course the division into two lateral cells is not found. Still more rarely is the one lateral half of the leaf only developed into an anther, the other retaining its leafy character; this condition is the type of the *Marantaceæ*, and occurs frequently as monstrosity in the conversion of the floral leaves into stamens, or of stamens into petals. In both cases, however, the course of the epidermis proves

\* The normal leaf, as is well known, exhibits upon its upper surface cellular tissue, different in structure from that on the under; to this we find that the pollen of the anterior and posterior cells of those compartments corresponds. It may perhaps be possible, and certainly not uninteresting, to ascertain by experiment, whether or not the pollen of one of these compartments only possess the external characters of pollen, and likewise different functions in the process of impregnation, or whether in Diœcious plants one kind would produce male, the other female embryos.

incontrovertibly (what is likewise established by the study of development) that the pollen forms itself in the interior of the leaf, and that therefore the anther cannot be considered as a leaf rolled up either backwards or forwards, which produces the pollen upon its surface.

If we carry back our investigations of the anther as far as its first appearance, we find that in every family it goes through just the same conditions, and that all the apparently deviating characteristics of this organ in the *Orchideæ*, *Asclepiadeæ*, *Cucurbitaceæ*, *Stylideæ*, &c., are merely later unfoldings of the same fundamental type, and are only physiologically unimportant modifications of the same plan, which nature, here as everywhere else where external differences of form only are concerned, has made the subject of so great and wonderful variety.

The formation of the pollen takes place in this manner: the four groups of cells intended for the pollen separate themselves from the remaining tissue of the leaf, their individual cells continually increasing, and in the interior of each probably for the most part four other cells are formed, in each of which a grain of pollen is produced, upon which the original cells become entirely reabsorbed. The four pollen grains often appear to be developed in one cell, if we decline the assuming that the delicate cells, closely surrounding them, have been overlooked. Sometimes, although seldom, there are only two grains of pollen found in the larger original cell, for instance, in *Podostemon ceratophyllum*, which in that case afterwards remain adherent one to the other, (figs. 29 and 30). Yet the quadruple number is undoubtedly the general rule, which explains the frequent occurrence of *pollen quaternarium*.

If, however, the reabsorption of the original cells does not take place, or is not perfect, a very peculiar arrest of development occurs, which being the constant type in the *Orchideæ* and *Asclepiadeæ*, has afforded botanists abundant occupation, whilst the entire peculiarity consists in this, that the pollen stops short at an earlier point in its development. This same condition may be seen as a temporary stage in the development of the flower of *Picea* and *Abies* in January and February, in *Pinus* in February and March, in which a loose waxy pollen-mass may be found imbedded in each division of the anther. At a somewhat later period we may see the four cells in *Picea* and *Abies*, in which the four grains of pollen lie closely united, and it offers a very pleasing spectacle when we observe under the microscope each grain expand itself by the absorption of water until it bursts its case in order to



escape, leaving the four cells emptied of their contents (figs. 25 to 28).

In this way we are enabled to recognise in the formation of the anthers only a stage in the development of the lateral organs of plants.

If we proceed further we next meet with the ovarium, the object and aim of the entire vegetable organization. In this we find all the constituent parts so closely condensed that their distinction appears very difficult, and it is here that the most extended stage has offered itself for hypotheses of all descriptions; indeed many have advanced the most extravagant speculations, relying upon their powers of guessing more than upon their talent of observation, by which it cannot be denied some fortunate hits have been made; of such Agardh's *Organographie* offers a series of capital examples.

According to the general, and at present commonly received view, the ovarium consists of buds (*ovula*), which develop themselves on the borders of leaves (*carpella*).

If we examine this view upon the usual grounds, we detect unfortunately a logical incorrectness in the reasoning which alone can be advanced and asserted in its support. And this is not the only case in which an entirely unfounded assumption has crept into science long ago, and which supported by tradition has been esteemed sacred and impregnable, so that no one has ventured to deprive the assumed deity of its veil, and show that this adoration had been prostituted before a vain puppet. We observe continually a sort of dread for the high authorities which first introduced such a doctrine; whilst in natural science nature herself should be the only lawful authority, and it is only in cases where she cannot be made subservient to our inquiries that any other testimony should be tolerated.

If we contemplate the entire range of the vegetable world we shall recognise this universal law, that a bud never forms itself on a leaf but from the axis of the plant or its derivative organs alone. If therefore the *ovula* are considered as buds, we must, as matter of course, conclude that the placenta is an altered axis. But what are the grounds which have been adduced in order to controvert this simple and necessary conclusion?

1. The well-known phænomenon in *Bryophyllum*; and
2. A monstrous development of gemmæ on the leaf of a *Malaxis* and an *Ornithogalum* observed twice.

The later case is an abnormal product, and therefore least of all suited to establish a general rule, which is in contradiction to all known phænomena, and which will, as well as

the other case, be presently explained. The first case constitutes, however, a singular exception. But I cannot help expressing a doubt as to its being really an exception, and would ask if the said leaf may not perhaps be a foliaceous expanded stalk. How long have such grounds been deemed sufficient to overturn a general rule, naturally deducible out of the principle of unity? It is further a recognised axiom in logic, that an hypothesis is by so much the more allowable, the easier it explains *all* phænomena connected with it, and the less it stands in need of other hypotheses for its support. Now I ask, in order to take an extreme case, what abnormal assumptions are not rendered necessary in the explanation of the true *placenta centralis libera* according to the usual mode, as, for instance, in the *Plumbagineæ* (figs. 20 to 23)? Here the five carpellary leaves would have been bent inwards, have united by their edges, then have separated themselves once more from their edges, would have again expanded, and then have united to one another anew; and lastly of at least ten ovula, nine would be abortive, the remaining one having in addition taken a remarkable position upon the summit of the central pillar; and be it remarked, all this would occur without the possibility of discovering even one step of so complicated a process in the plant itself. It would indeed be universally necessary to have recourse to the supposition of an abortion in all uniovulate ovaries, a circumstance not in the least corroborated by an appeal to nature.

The second and opposite case is however almost more dangerous still as respects the usual view; for when the entire surface of the carpellary leaf bears ovules, as is the case in the *Gentianeæ*, *Nymphæaceæ*, *Butomeæ*, &c., I know of no tenable explanation of this phænomenon deducible through the common hypothesis. This has made it necessary to have recourse to many explanations; sometimes the ovula are represented as formed on the edge of the carpellary leaf, sometimes on the central nerve\*, and sometimes on both.

\* Thus in a work by a M. Eisengrein, entitled "*Die Famili der Schmetterlingsblüthigen mit besonderer Hinsicht auf Pflanzen-Physiologie*," it is advanced as a law that in the *Leguminosæ* the ovules are formed on the middle nerve. Independently of the circumstance that the position of the different parts of the flower shows that in this family the convoluted borders of the leaf are the seat of the ovules, M. E. might easily have convinced himself of the uselessness of his lengthy observations, had he taken the trouble to examine a bean-bud with a tolerably strong magnifying glass. I feel indeed disposed to consider the book altogether as a pathological symptom of the spirit of the age. It combines the most barren trifling with empty comparisons, in the style of a modern, but already expiring school, and this is put forth as philosophy! The book discloses a little investi-



In this manner an extravagant view has been thrust upon the science, founded upon the weakest possible grounds, the circumstance itself been loaded with difficulties, and the natural condition most completely neglected. We shall see further on how easy is the explanation of the only apparently contradictory fact of the *placenta parietalis*, by the assumption that the placenta is a formation of the axis (*Axengebilde*), which indeed may be proved, without the assistance of hypothesis, from the well-known modifications of the stalk. But if we pass over to the investigation of nature, we find—to commence with the most simple conditions—that each individual carpellum is at first quite isolated, constructed similarly to every young leaf or lateral organ of the plant. It is not until a much later period of their development that it begins to direct its edges inwards when the carpellum is closed, or to adhere to the neighbouring edges when the pistil is *unilocular* and *many-leaved*.

Amongst those families which in this respect again deviate from the ordinary plan, must be included the *Gramineæ* and *Cyperaceæ*. In both families their development shows that the ovarium consists of *one* carpel only. In both families the two anterior\* stigmata for the carpel are merely a further development of the *ligula*; the posterior, however, which is so often abortive in the grasses, is analogous to the surface of the leaf, and the ovarium itself to the sheath of the leaf.

We can now take a review stage by stage of the entire development of the pistil, from its first appearance as a flat foliaceous organ, until it becomes divided into ovary, style, and stigma. This will enable us to obtain a correct idea of these parts, for which little has hitherto been done, as organs whose use and function, completely different, have received the same name.

The ovarium then is that portion of the leaf which incloses the *ovula*; the style, that portion which is rolled up and does not develop *ovula*, whose object is to conduct the prolongation of the pollen tubes; and lastly, the stigma is the free termination of the superior part, whose object is to receive and hold the pollen.

This result is attended again with manifold consequences. We find in the nomenclature of organs, for instance, that en-

gation of living nature as of the “physiological principles” paraded in the title; and the author shows himself to be at least thirty years behind the most common-place botanical works of the present day, and even not *au niveau* with such men as Grew and Malpighi.

\* If the ovarium be viewed in a direction from the axis.

tire families to which styles had been ascribed, as the grasses, possess *stigmata sessilia* only. Some few species belonging to these families, as *Lygeum* and *Zea*, possess an actual style. It has always appeared singular to me that the same botanists who, on the one hand, have advanced the position that the styles offer the surest means of determining the number of the carpels, because every carpel has its corresponding style, should, on the other hand, have ascribed only one carpel to the grasses, although they at the same time speak of several styles. A true style occurs equally seldom in the majority of the family *Euphorbiaceæ*; indeed in *Euphorbia*, *Ricinus*, *Andrachne*, *Crotophora*, &c., in which more than one style has been described, there is either none at all, but merely *stigmata sessilia bifida*, or only one style present, as for instance in *Euphorbia*, in which three carpellary leaves are united superiorly so as to form a tube, although a short one. We find the style also to be deficient in most of the *Alismaceæ*, *Malvaceæ*, *Phytolaceæ*; they possess only stigmata: in some of these plants, for instance *Ricinus* and *Phytolacca*, the so-called surface of the stigma sinks down with its papillæ as far as the basis of the carpel-leaves. It is equally incorrect to speak of *rami styli* in the *Compositæ*, which are in fact only forms of the double-lobed stigma. Hitherto little more than a traditional meaning has been applied to the words style and stigma, and this has been still more corrupted by means of pretended logical distinctions. It will, however, be easily seen that if botany is to be treated in a really scientific manner, the terms must be based upon ideas, which being derived from the nature of the vegetable structure, imply certain actual organic differences, and can be adopted in a sense so strict as to avoid the possibility of including the most various things under the same term; or on the other hand of separating identical organs by giving them different terms. The prosecution of the inquiry into the process of development also very simply settles the old dispute as to whether the style possesses a canal or not. Since each style is formed either by the rolling together of a single leaf (apocarpous fruit, Lindl.) or through the union of the edges of many leaves (syncarpous fruit, Lindl.), it must always possess a canal, which certainly cannot be always recognised as a cavity upon making a section of the style in the open flower, since the internal layer of cellular tissue (*Tissu conducteur*, Brongniart, properly speaking the epidermis of the upper surface of the leaf,) becomes so expanded through alteration in the form of the cells and the exudation of mucus in the intercellular spaces, that the individual cells become completely detached from their connection,



and lie loosely imbedded in the mucus, as for instance in the *Orchideæ*, many *Liliaceæ*, &c.

These are then the important points from which nature does not deviate in the vegetable organization, whilst she manifests the greatest possible variety in regard to the external differences of form. The form of the stigma exhibits the most wonderful variations of shape, and upon this account has been of all parts that most frequently misunderstood. The style also, and even the carpel-leaf, offer many varieties, especially the latter, from the formation of spurious septa by cellular excrescences, as in the *Aroideæ*. We find further that the carpel leaf in the *Coniferæ* is not closed; in the *Resedaceæ* three are united to form one open basin, strictly closed in most families, frequently bent inwards towards the axis, and then turned backwards again, so that the placental portion forms a belly, and the style *appears* to spring from the base, where the transitions of development may be studied, beginning with the *Euphorbiaceæ*, through the *Phytolaceæ*, *Alismaceæ* as far as the *Borragineæ*, and *Labiataæ*, and lastly in the entire family of the *Dryadeæ*. The young ovarium in the *Labiataæ* and *Borragineæ*, for instance, is usually a two-leaved carpel (fig. 2), whose edges however are very soon joined to form the style; and by the development of the ovulum the part inclosing it becomes expanded both above and below, whilst the style, the upper end of the leaf, is incapable of this elevation and distention. The fruit of the palm presents a very similar appearance, in which the embryo stands at first erect soon after impregnation has taken place; as the seed however advances to maturity, the inner side of the ovarium does not enlarge with it: thus the point of the embryo becomes fixed and serves as a central point, about which the *radicula* describes a quadrant, to which figure it is limited by its partial development: in this manner is formed the *embryo horizontalis lateralis*. There has been a great deal of time lost in the discussion of such apparent abnormalities, which would not have been the case had surmise not taken the precedence of investigation.

If we now turn to the *placenta* and *ovulum*, and, which will be the most advantageous course to pursue, commence with the simplest form, we shall select that where no carpellary leaf is present, which is without doubt the one of all others that presents the most insurmountable difficulties if attempted to be explained according to the usual theory. This state is found in *Taxus*, for instance, where the entire female flower is nothing else than the terminal *leaf-bud* of the axis to which it belongs. The leaves are arranged in the customary spiral

direction, even to the extreme summit, and no one leaf implies in the slightest degree an adaptation to the female part more than another (fig. 1). The axis, as is customary, terminates here also in a small protuberance (the *punctum vegetationis* of Wolff), and this is the *nucleus* of the ovule. Thus the axis forms the second antagonistic power (*differenz*) of the plant, forming as it does the female portion, and we are now in a condition to perceive that impregnation and fructification consist in the conjunction and balancing of the two most important antagonistic forces the plant possesses, viz., those of the horizontal and vertical structure.

We will however calmly prosecute the course of our investigation further. The terminal portion of the axis constitutes therefore the *nucleus* of the ovule, and is the *only actual* and never-failing portion of the entire female organ, whilst all other parts are or may be partially deficient; some in this plant, some in that. Now this end of the axis is frequently found bent, so that its point becomes reflected upon itself (*ovulum anatropum*), and adheres to that portion which retains its proper direction (*raphe*), a process which may be easily recognised on inspection. In this condition (*ovulum ex nucleo nudo constans*) we find the ovule in many families, as for instance in the *Santalaceæ*, *Rubiaceæ*, *Dipsaceæ*, *Cuscutæ*, *Asclepiadeæ*, &c.\*

There is indeed no reason why the nucleus may not be developed without suffering this reflexion of its axis, (as *ovulum atropum ex nucleo nudo constans*,) although I have never yet met with an instance of the kind.

The formative power concentrates itself in such a manner around this extreme point of vegetation that what subsequently appears as separate lateral organs is here consolidated in the shape of a sheath-like envelope. These leaves inclosing the stalk of the last bud are termed *ovular membranes*, and are distinguished by the total absence of spiroidal vessels, which are proper to the *raphe*, or that portion of the ovulum which is not divided into nucleus and integument; the presence of these vessels therefore would show that the membrane under examination was only an apparent ovular membrane. Still it sometimes happens that at a much later period—after fructification has taken place—vascular bundles may be detected in the actual integuments; this is, however, very rare indeed.

\* R. Brown includes the *Apocynæ* also under this head; but they have a simple integument. In these, as well as in the *Asclepiadeæ*, it is not the nucleus which becomes developed in the interior after impregnation, but the sac of the embryo, which becomes at an early period filled with opaque albumen, which is visible after impregnation as a dark kernel perceptible through the integument.



Now such a simple envelope (*integumentum simplex mihi*)\* is found under these circumstances :

1. Without the axis being bent (*ovulum atropum cum integumento simplici*) in *Taxus* at the flowering time, in the *Cupressineæ*, *Juglandæ*, and *Ceratophylleæ*.

2. Or else the axis suffers the reflexion above described, whereby the envelope becomes adherent to the prolonged axis (*raphe*); (*ovulum anatropum cum integumento simplici*). To this class belong the *Abietineæ*, *Synanthereæ*, *Lobeliaceæ*, *Campanulaceæ*, *Goodenovieæ*, *Lentibulariæ*, *Scrophularineæ*, *Orobancheæ*, *Gesneriæ*, *Sesameæ*, *Labiataæ*, *Bignoniaceæ*, *Polemoniaceæ*, *Convolvulaceæ*, *Solaneæ*, *Borragineæ*, *Gentianeæ*, (including the *Menyantheæ*, which have likewise only one integument; for the external hard covering, separable from the ripe seed, is nothing more than the epidermis of the integument, whose cells have become much lignified); further the *Apocynæ*, *Umbelliferæ*, *Ranunculaceæ*, *Loaseæ*, &c.

Lastly, there is a second covering formed, which incloses the point of the axis (*integumentum externum et internum mihi*), and here also both modifications may occur.

1. The axis remains straight, as for instance in the *Polygonæ* (fig. 4), *Cistineæ*, *Urticeæ*, and a portion of the *Aroideæ*.

2. Or else the axis becomes bent upon itself, adhering to the external integument (figs. 20 to 23). In the remainder of the family of the *Aroideæ* may be observed all possible states of transition, from an elongated axis, the reflected portion of which, with its integuments, hangs free (as is also the case in *Rafflesia* according to R. Brown), to the complete adherence, in which case the unreflected portion of the axis appears as *raphe*. Further, we must include amongst these *all* remaining monocotyledonous plants. R. Brown has not indeed expressed himself in positive terms on this point with respect to the *Orchideæ*; they possess, however, decidedly both integuments, which are only to be observed in their earliest stages (fig. 5), since the embryo sac having been very early developed has at the time of impregnation almost entirely compressed the *nucleus*, so that one would be induced to consider the very thin integument as the *membrana nuclei*. I will content myself with adducing the following among the dicotyledons as examples, to avoid occupying too much room with the mere enumeration of names, *Nymphæaceæ* and *Cabombeæ*, the *Plumbagineæ*, *Resedaceæ*, *Passifloræ*, *Caryophylleæ*, and *Cruciferaæ*.

\* I feel myself obliged to abandon the usual terms *testa* and *membrana interna* and others which are taken from the ripened seed, and are nowhere applicable, and which would only tend to confuse ideas of things on account of the many errors historically attached to them.

Mirbel was the first who published any detailed account of the general formation of these integuments of the *nucleus*; but although he has partially observed the phænomena accompanying their formation, he has evidently been far from understanding them, and could not therefore clearly explain the process; and it is indeed scarcely possible to collect from his own words what was his real opinion of the matter. We are indebted to R. Brown, who has struck out so many new paths in this and every other department of botany, for the first correct account of their mode of formation in the *Orchideæ* in 1831, and at a later date (in 1834) in his dissertation on the female flowers of the *Rafflesia*\*, in which he extended his observations to many other families. Fritsche has however furnished the most detailed account of this subject in Wiegmann's *Archiv*, but he has confined his observations entirely to one species, and that the least favourable to such an investigation on account of its compressed growth and anatropous ovule. He has also neglected to take accurate micrometrical measurements, a point of the utmost importance here, by which alone he would have been able to avoid some errors. Thus, for instance, the expansion of a cylinder underneath a given line, and its contraction above it, are circumstances which can only be ascertained in objects so minute by means of comparative measurements, since, of course, every stage of the process cannot undergo examination at the same time, and these differences are of the greatest importance to the true appreciation of the subject. In this manner Fritsche has fallen into the error, on the one hand, of supposing that both integuments are a simultaneous formation produced by the inflexion of the first fold into the body of the ovule, and on the other hand he has viewed the formation of the inner integument in too confined a manner, as a mere fold of the *epidermis nuclei*.

The plan which nature adopts is simply this:—The example I shall select is that of the atropous ovule, for instance of the *Polygoneæ* (fig. 4), as being the most simple. At a certain distance below the apex of the original protuberance an ideal line may be recognised, intended as the basis of the *nucleus* (fig. 4 *b.*), which does not afterwards increase in thickness. Above this line the apex forms itself into the *nucleus*, and below it the substance of the axis expands and forms a protuberance (fig. 4 *b.*), which extending itself as a kind of membranous fold gradually covers in the *nucleus*. (*Integumentum primum aut internum* mihi; *Secondine* Mirb.; *membrana in-*

[\* Account of the results of Mr. Brown's researches on these subjects will be found in Phil. Mag. and Annals, N. S. vol. x. p. 437, and Lond. and Phil. Mag., vol. v. p. 70.—EDIT.]



*terna* auct.) Sometimes soon after, and indeed almost contemporaneously with this, sometimes later\*; sometimes immediately below the first protuberance, at other times at some distance from it (as for instance in many *Polygoneæ* and *Cistineæ*), we may next observe a second protuberance, which, as the second integument†, covers in the first. (*Integumentum secundum sive externum* mihi; *Primine* Mirb.; *Testa* auct.) The first-formed integument certainly does frequently consist only of a fold of the *epidermis* of the *nucleus*; nevertheless we do find a tolerably thick parenchyma taking part in its formation in almost all those families which form no second integument, and also in some which possess both coverings, as, for instance, in the *Euphorbiaceæ*, *Cistineæ*, and *Thymeleæ*. In the case of these three families, a peculiar process takes place, namely, upon the seed becoming ripe the external integument is gradually absorbed, until nothing but a thin membrane is left, usually described as *epidermis testæ*, or in the *Euphorbiaceæ* it has been given as *arillus*; and on the other hand, the actual modified *epidermis testæ* has also been described as the *arillus*, for instance, in the *Oxalideæ*. The apex of the original papilla, which develops itself as *nucleus*, varies exceedingly in its size in proportion to the entire ovule, if examined in the different families. It often forms a long and nearly cylindrical body, as in *Loasa* and *Pedicularis*; in many cases it is shorter, so that that portion of the ovule in which no distinction has taken place between nucleus and integument (the whole being like a fleshy distended stalk), is by far the more predominant, as in all the *Synanthereæ*, *Canna*, *Phlox*, *Polemonium*: it consists again, in some instances, merely of the extreme point of the papilla itself, as in *Convolvulus*; or nothing more than an ideal point remains, which can no longer be distinguished as an independent body, above which, however, a protuberance develops itself, and thus forms a micropyle, as in the *Dipsaceæ*.

Of course the process I have been describing becomes considerably modified in individual points, either through the unilateral development of the ovule (*ovulum campylotropum* Mirb.), or through the reflexion above described (*ovulum anatropum*).

\* This is most conspicuous in *Taxus*, in which the second integument (fig. 1 b.) does not exist until after impregnation has taken place (*cupula* auct).

† I observed this to occur very distinctly in *Hydrocharis* and *Valisneria*; and, as Richard's analysis shows, all other true *Hydrocharideæ* have atropous ovules. Endlicher's attribution of an anatropous ovule to this family (*Genera Plantarum*, p. 160) is probably derived from a partial investigation of *Stratiotes* (which perhaps does not belong here), and which has been extended to the remainder of this family.

I should however be far exceeding the limits assigned me were I to insert here a detailed account of the numberless individual peculiarities which I have met with in the course of my observations. I will content myself with remarking that the *Quartine* of Mirbel does not exist: what he describes is nothing else than a temporary *endosperm* in those families, in which the embryo sac displaces the entire *nucleus* at an early period, although it is not destined to form *albumen* at a later period by means of a permanent endosperm.

These integuments experience manifold changes during the ripening of the seed, so that the original number can seldom or never be recognised in the ripe seed. Sometimes all the integuments become consolidated so as to form but one; at other times, and this is more frequently the case, the integuments become separated into different layers of cellular tissue, of various degrees of development, in which case the homogeneous tissue can easily be separated from the heterogeneous. In this manner the integument of the ripe seed may sometimes be divided into as many as five layers, although only one or two membranes, or, as in *Canna*, no complete integuments were originally present. But since it frequently happens that the greatest variety may occur in the ripe seed in this particular in one and the same family\*, as has been already related of the group *Menyantheæ*; whilst, on the other hand, the entire absence, or the presence of one or two integuments in the ovule appears to be very constant in the different families and groups, it may possibly be more advantageous to return entirely to the old terminology of Richard, and only speak of an *episperm* in the ripe seed, the different positions of which may then be more minutely characterized, whilst at the same time greater accuracy may be observed in the description of the ovule. Many interesting results may probably be ascertained when these investigations shall have been extended over all the families; already the small circle of my own observations has afforded many hints. It is remarkable, for instance, that *not a single* monocotyledonous family possesses fewer than two integuments, and the first impression caused by a review of the different families given above is, that amongst the dicotyledonous the majority of the monopetalous families is furnished with but one integument, whilst the polypetalous generally possess two.

Although we cannot remain one moment in doubt that in plants possessing a true *placenta centralis libera* (still

\* Indeed in the same genus. Thus one portion of the *Salviæ* possesses spiral cells in the epidermis of the integument of the seed, and in the remainder they are absent.



less in such where, as in the *Polygoneæ*, *Taxus*, *Juglans*, *Myrica*, the placenta cannot be supposed to exist as a separate organ), the *nucleus* of the ovule is only the summit of the axis, yet the question suggests itself as to how the parietal placenta is to be understood; and I do not consider the explanation to be very difficult. We find in many of the *Aroideæ* that the axis is spread out at its summit, forming a kind of disc; upon this surface are a number of buds as ovules, similar to the arrangement which is found, in the *Synantheræ* and other families, to take place among the flower-buds; we next observe these discs expanded into lobular processes, and adherent to the edges of the carpellary leaves in all parietal or pseudocentral placentæ, a modification of the axis which is met with in *Dorstenia*, the parietal placentæ may be explained equally well, and perhaps with greater simplicity and consistency, as a mere ramification of the axis. It will not therefore surprise us, that the buds of these branches (*ovula*) grow only upon their inner side, viz., that directed towards the axis, since the same is observed in the inflorescence of many plants, for instance, in *Æsculus*. Lastly, we find the axis expanded somewhat in the shape of a basin in those plants in which the entire wall of the simple ovarium is occupied with ovules, as may also be seen in the similar modification of the stalk in many *Rosaceæ* and in *Ficus*. There cannot however be any reason adduced why such deviations in the form of the axis should be assumed as occurring in a lower internodium between the leaves and bud, whilst they are denied existence in a higher one between the carpellary leaves and ovule-bud, or are said to be impossible.

But we find in nature, that in parietal placentæ the edges of the leaves are never laid upon one another in their entire length, and adhere in that manner, but become united from below upwards by the subsequent growth of a more or less distinctly interposed substance. This interposed substance is very evident in the *Fumariaceæ* and *Cruciferaæ*, in which it appears much later than the carpellary leaves, stands exactly within them, and in the latter family forms the spurious partition, by its gradual extension towards the middle and its subsequent adhesion. The placenta shows itself to be independent of the carpellary leaves, during its growth, most strikingly in the *Abietineæ*. My investigations of the earliest conditions have shown me that the organ which, since the researches of R. Brown, has been considered as an open ovarium, is only a scale-like expanded placenta, and that the organ which R. Brown has named *bractea* is the actual carpellary leaf (fig. 18). This result has been confirmed to

me in a most beautiful manner by a cone of *Pinus alba*, found this spring, which upon the upper half was covered with female and upon the lower with male flowers. In the *Abietineæ* the placenta, left without the least constraint, develops itself to such an extent, that at length the carpellary leaf itself appears as a mere supplementary part. The more extended detail of these investigations being here out of place, I must beg to refer to a work on which I am at present engaged, upon which I have been occupied some years with great interest, and which is intended to include the perfect history of vegetable development in every department.

In all this variety of forms of the ovulum-bearing axis, whether it grows upwards upon the carpellary leaves or elevates itself free in the middle, there frequently occurs the additional peculiarity, that besides the reflexion sustained by the axis, which has been so often alluded to, there is another to which it is subject in consequence of the space being too limited superiorly for the development of the ovular-bud; the *ovulum horizontale* and *pendulum*, with their various intermediate states, are hereby formed. This modification, however, proceeding, as it appears to do, merely from an external necessity, viz., the extent of space allotted to it, is of far less consequence than the first-mentioned reflexion; and we find accordingly in one and the same family (in the *Dryadeæ*, for instance) both pendent and erect ovules, but it seldom occurs in a highly developed family, and probably only in the *Aroideæ*, that atropous and anatropous ovules are found together. For this reason the definition of a *radicula supera* or *infera* in botanical descriptions possesses little or no value, when regard has not at the same time been had to the internal formation of the ovule.

As we found that there was a peculiar development of the cellular tissue in the anthers, by means of which the leaf becomes converted into an organ for the production of pollen, so we observe also that there is a peculiar modification of cellular tissue in the summit of the axis or *nucleus*, by which it likewise becomes adapted to the taking on of a new organism. One of the parenchymatous cells, namely, develops itself to a much greater extent than the others, indeed out of all proportion, since it becomes subsequently converted into the sac of the embryo. This takes place in all Phanerogamia without exception, and at a period long previous to impregnation; no more than this, however, constitutes the essence of this formation. In other respects this sac is subject to the most manifold varieties: 1. In relation to form, being sometimes round, sometimes oval, cylindrical, bottle-shaped, or sometimes fiddle-



shaped, or, as in *Lathræa squamaria*, where the excavations are shapeless. 2. In relation to the point of the nucleus, which is sometimes nearer, at other times further off. 3. As to contents, at one time clear as water, homogeneous and fluid, at another opaque and granular, and sometimes cellular. 4. With respect to the time of its formation, whether a longer or shorter interval before the opening of the flower. And lastly, in the greater or less compression of the nucleus. But a treatise may easily be written concerning the varieties of the embryo-sac previous to impregnation.

We have now proceeded so far in the process of development of the plant that we already stand at the door of the sanctum. The process by means of which the new organism should be formed out of the parent plant, remained during a very long time an object of the fantastic sports of the imagination, or of falsely-grounded analogies taken from the animal kingdom, which arose partly from the impossibility of actual observation on account of the imperfection of instruments; until at length Amici, Brongniart, and R. Brown threw an entirely new light on the matter by their beautiful discoveries. Yet the most important part of the secret remained undisclosed. I have prosecuted and repeated with untiring zeal the discoveries of those great men, and have not only found the most important of their individual observations confirmed as general laws, but believe that I have advanced a not unimportant step in the inquiry. I have followed the pollen-tubes (*pollen-schläuche*) already in so many (upwards of 100) different families, with the most patient investigation from the stigma into the ovulum, that there can be no doubt concerning this being the general process in all Phanerogamia. R. Brown has described more than one pollen-tube as entering into one micropyle; I have observed two to three in many plants—in *Phormium tenax* three to five, in *Lathræa squamaria* scarcely ever less than three, and once even seven.

If the pollen-tubes be followed farther into the ovulum, a process perhaps the most delicate that occurs in botanical investigations (fig. 3 and 24), it will be found that usually only one, rarely a greater number\*, of the pollen-tubes entering into the micropyle penetrates the intercellular passages of the *nucleus* and reaches the embryo-sac, which being forced forwards presses it, indents it, and forms the cylindrical bag, which has already been described, in the commencement of this paper,

\* As is the case in the regular and accidental *Polyembryonatae*, to the latter of which the genus *Cynanchum* especially belongs. In the summer of 1835 I found *Cynanchum nigrum et fuscum* to contain from two to five embryos in at least every third seed.

as constituting the embryo in the first stage of its development, which consequently consists solely of a cell of leaf parenchyma supported upon the summit of the axis. It is therefore formed of a double membrane (excepting the open radicular end), viz. the indented embryo-sac and the membrane of the pollen tube itself (fig. 12, 13.). I can from direct investigation refer for corroboration of this fact to the following species: *Taxus*, *Abies*, *Juniperus*, *Lathræa*, *Phormium tenax*, *Canna Sellowii*, *Oenothera crassipes*, *Mirabilis longiflora* and *Jalappa*, *Veronica serpyllifolia*, *Limnanthes Douglasii*, and less evidently in *Martynia diandra* and *Cynanchum nigrum*; on the other hand most beautifully clear in *Orchis Morio* and *latifolia*. In all these plants I have observed the entrance of the pollen-tube into the embryo-sac and the gradual conversion of its end directly into the embryo; and in *Taxus*, and very easily in *Orchis*, I was even able to withdraw that portion of the tube which represented the first stage of the embryo out of the embryo-sac and that indeed at a tolerably advanced period\*.

\*“ In order to meet any objections which may be made by those who have had no opportunity of examining these subjects more closely, I will just remark, *en passant*, that Corda’s history of the development of the *Coniferae*, (*Acta Leop. Carol.*, xvii. pars 11,) coincides with Nature in the fewest points possible. It has caused me much pain, on account of some eminent men, who, having neither opportunity nor time to examine into the case, and judging of others by their own conscientiousness, have allowed themselves to be led into a precipitate admiration. It is however, in this case, impossible to absolve them from all blame, since the memoir exhibits its character openly enough. For in the first page it is stated: ‘ Since the appearance of Robert Brown’s writings, and his journey through Germany, every one is acquainted with the general results of his observations, so that I consider it superfluous to give, in this place, an accurate account of them.’ Now it is well known that Mr. Brown had already published, in 1832, his discovery of the entrance of one or more pollen tubes into the micropyle; and those persons who had the good fortune to meet with Mr. Brown, during his journey through Germany (in 1833), will remember that he carried with him impregnated ovaria in spirits, and with his accustomed kindness showed the entrance of the pollen tubes into the ovulum to every one who took any interest in the subject. Notwithstanding this, Corda, a few lines lower down, affects an unpardonable ignorance of this fact, in order to arrogate to himself a discovery which Amici (already in 1830) and Mr. Brown had made long before him. Inconsistencies are also evident in the figures. Fig. 14, for instance; the embryonal sac is termed *nucula*, (should be *nucleus*,) and the pollen tubes enter it in order to produce, by their emissions, heaven knows what kind of an imaginary figure. Fig. 22: here the embryonal sac is even called embryo (E), and the pollen tubes run around it. But



The tracing of the pollen-tube into the interior of the embryo-sac is not so easy in all plants, because the cells of the nucleus which are arranged around the summit of the embryo-sac are very firm and opaque, so that it and the pollen-tube cannot be exhibited quite free. In these cases, however, three circumstances speak for the identity of the embryo with the pollen-tube: 1st, the constantly equal diameter of the latter exterior to the embryo-sac and of the former just within it. 2nd, The invariable chemical similarity of their contents shown by the reactions produced on the application of water, oil of sweet almonds, iodine, sulphuric acid, and alkalis. The general contents of the grain of pollen granule is starch; and this either proceeds unchanged downwards through the pollen-tube or else passes along, being previously changed by a chemico-vital process into a transparent and colourless fluid, which becomes gradually more and more opaque and is coagulable by the application of alcohol: out of this, by an organizing process, the cells are formed which fill the end of the pollen-tube, extending in *Orchis Morio* far beyond the ovule, and thus form the parenchyma of the embryo: but I should exceed the limits of this essay were I farther to follow up the formation of these cells. 3rd. Lastly, the identity of the embryo and the pollen-tube is farther supported by the fact, that in such plants as bear several embryos there are always precisely the same number of pollen-tubes present as we find embryos developed.

The most important result of these facts, and which I shall not now attempt to carry out in its full extent, but content myself with alluding to, is that the sexual classification hitherto adopted in botany is directly false. For if the ovulum be understood in physiology to represent that material foundation from which the new being becomes immediately developed, and if we term that portion of the organism in which this material commencement is deposited before it becomes developed *the female organ*, whilst that part which calls into action or promotes the development of the germ by means of its potential effects is termed the *male organ*, it is evident that the anther of the plant is nothing but a female ovarium and each grain of pollen the germ of a new individual. On the other hand, the embryo-sac only works potentially,

it would be an herculean task to follow, step by step, this memoir. It will here suffice to observe that, with the exception of a few points of minor importance, everything almost surpasses the limits of possible error, and does not in the least represent nature. I refer every one, who has even but little practice in such examinations, to nature herself, as the observations are not of the most difficult kind."

determining the organization and development of the material foundation, and for this reason therefore ought to be termed a male principle, were we not to consider, perhaps more correctly, (without embarrassing ourselves with lame analogies taken from the animal kingdom) that the embryo-sac merely conveys new organizable fluids by means of transudation and thus only serves the office of nourishment\*.

Secondly, the process of the development of the embryo, already described, easily establishes the fundamental unity of the Phanerogamia and those Cryptogamia in which the sporules are evident conversions of the cellular tissue of the foliaceous organs or leafy expansions, since the same part in both furnishes the groundwork of the new plant in both groups, and the only difference existing between the two is this;—in the Phanerogamia a previous formative process in the interior of the plant precedes the period of latent vegetation, whilst in the Cryptogamia the sporule (the grain of pollen) develops itself to a plant without previous preparation. Difficulties nevertheless occur here in the consideration of Mosses and *Hepaticæ*, and more particularly in the enigmatical *Rhizocarpeæ*. It appears to me, however, that in this last-named family especially, there still remains much to be observed.

Lastly, this detailed process explains simply and naturally the formation of buds on leaves, although it so seldom occurs (whether it shows itself as a peculiarity of the plant or is an abnormal phænomenon), as being merely a partial retrogradation into a lower (cryptogamic) organization.

In closing this brief exposition I must subjoin a few remarks, partly for the purpose of anticipating unjust interpretations, and partly to afford a more correct apprehension of this essay.

In the first place, I am far from meaning to lay claim to all the views which have been developed in these pages as my own discoveries; I desire to give every one his due; and not laying so very great value on mere priority, I consider it much more honourable in founding a new view to extend it over the entire department of the science and render it insubvertible by patient investigation, than merely to be the discoverer of something new, in which good fortune so often

\* The embryo-sac retains this nourishing function in most of the albuminous seeds until a later period, that of germination, for nutriment accumulates in the cells, which gradually fill up the whole of the interior of the embryo-sac, which becoming afterwards converted into fluid is appropriated to the demands of the young plant. In the seeds which have a central albumen (the *embryo periphericus*), the albumen is merely a residuum of the *nucleus*, and the space which was occupied during the earlier stages by the embryo-sac is now entirely occupied, in the mature seed, by the embryo alone.



plays the most conspicuous part. The narrow limits afforded to a memoir of this nature, and not any want of information as to what and how much various celebrated men had communicated to the public before me, has been the cause of my entering so slightly into the historical detail of all that has been done in this branch of science. These points, together with the perfect completion of my investigations, I withhold until the appearance of the work above alluded to, from which my only intention was to give here a small portion of the results.

On the other hand, I must remark, secondly, that everything which I have included here is the result of my own investigation, and I have not received the smallest point, even upon the best authority, without myself proving its correctness.

Thirdly and lastly, I must state that everything I have put forward is the result of actual observation, and that speculation (immediate consequence in its strict logical sense excepted) has not had the least share in these observations. Whatever of interest occurs that can lay claim to novelty has been known to me for years, but I postponed its publication in order to afford me time to take the utmost advantage of the numerous and valuable resources which were placed at my disposal in Berlin, in order to give my work such an extension that the results may not appear as isolated facts, but assume the shape of laws for the entire vegetable organism.

It is of course evident that I could subjoin but few drawings, necessary in explaining some of the most important points of my investigation; and I will only hope that by reason of this deficiency I have not become too frequently unintelligible.

I am only desirous of having such persons as judges of my work who have recourse to nature as umpire, and who have no other object in view than *Truth*, the only praiseworthy motive in scientific pursuits and which alone has been my guide in all my investigations; if by this I have been the means of contributing but a little to the cause of science, I shall consider myself as eminently fortunate.

————— si quid novisti rectius istis,  
Candidus imperti; si non, his utere mecum.

*Appendix.*—I have referred frequently in the course of the foregoing treatise to *Lathræa squamaria*, which I have done in preference to other plants on account of the clear and evident manner in which I have seen many parts in this. Now it has just met my eye that Unger (*Beiträge zur Kenntniss*, etc. *Ann. der Wiener Mus.*, vol. ii. p. 50,) denies the existence of cotyledons and radicle in the embryo of *Lathræa*; any one may therefore naturally object that I have selected but

a poor subject as an example. I must, however, confess that I cannot comprehend Unger's assertion, for the embryo of *Lathræa* has such evident cotyledons that they may clearly be perceived with the help of a lens of from six to eight times magnifying power, and an acute observer may recognise them without the aid of a glass. The cotyledons are at least equally long with the other parts of the embryo, as they have been figured by Gærtner. I can scarcely imagine, I must confess, that Unger should have entirely overlooked the embryo and have taken the very firm albumen for it. Generally speaking, the acotyledonous plants must not be understood as forming a third division in opposition to the monocotyledonous and dicotyledonous, and indeed the importance of this characteristic is very subordinate; it is a phænomenon which may occur in every sort of plant. The matter consists merely in the period of latent vegetation commencing somewhat earlier, whilst the completion of the embryo in the fruit only proceeds as far as the point, where it becomes of a globular shape; but the farther development passes over the fruit into the germination, as is the case in the entire family of the *Orchideæ*.

In page 51 Unger expresses his opinion that the *Orobanchæ* should be united to the *Labiataë*; now the construction of the ovarium is precisely the distinctive character of the *Labiataë*, and which is wanting in the *Orobanchæ*. On the other hand, *Lathræa* (which likewise possesses stomata) and *Orobanche* agree so completely with the *Scrophularineæ* in every respect excepting the habitus, solely to be ascribed to their locality, that I cannot find anything like a sufficient ground to keep them disunited. It would certainly not occur to any zoologist to separate an animal from its natural family merely because it was a parasite: wherefore then should it be otherwise with the vegetable kingdom\*?

### *Explanation of the Engraving (Plate III.)*

Fig. 1. A longitudinal section of the flower-bud of *Taxus bacca* (femina). *aa.* leaves. *b.* the rudiment of the second integument, which forms the berry. *c.* the first or inner integument. *d.* nucleus. I have represented the course of the epidermis by a fine line upon the ovule and the two interior leaves, as likewise in figs. 4, 18, 22, and 23.

Fig. 2. Longitudinal section of a very young pistil of *Salvia Clusii*. *a.* carpellary leaves. *b.* ovule. *c.* canal of the style.

Fig. 3. The inferior portion of a newly impregnated ovule of *Mirabilis longiflora*, also a longitudinal section. *a.* funiculus. *b.* remains of the nucleus. *c.* integumentum simplex. *d.* embryo-sac. *e.* pollen-tube, whose extremity expands to form the embryo. *f.* an abortive pollen-tube.

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[\* On this subject see Dr. Lindley's paper on the Botanical Affinities of *Orobanche*, in Phil. Mag. vol. xi., p. 409.—EDIT.]



Fig. 4. Longitudinal section of a young ovule of *Polygonum orientale*. *a.* nucleus. *b.* protuberance out of which the *integumentum internum* is formed. *c.* commencement of the *integumentum externum*.

Fig. 5. A very minute ovule of *Goodyera procera*. *a.* integument. *extern.* *b.* integum. *intern.* *c.* remains of the nucleus. *d.* embryo-sac.

Fig. 6 and 7. Early conditions of the embryo of *Potamogeton lucens*.

Fig. 8. *Potamogeton heterophyllus* at a later period than the preceding. *a.* plumula. *b.* cotyledon which is still unclosed (*ungeschlossen*).

Fig. 9—11. Different grades of development of the embryo of *Echium vulgare*. *a.* embryo-sac. *b.* embryo.

Fig. 12. Summit of the embryo-sac of *Phormium tenax* with the embryo in course of development. *a.* embryo-sac. *b.* pollen-tube. *c.* embryo.

Fig. 13—17. Formation of the embryo of *Ænothera crassipes*. *a.* embryo-sac. *b.* pollen-tube. *c.* embryo. *d.* terminal shoots (*punct. vegetationis*, Wolff). *e.* cotyledon.

Fig. 18. Longitudinal section of the female flower of *Pinus abies*, from a cone about three quarters of an inch in length. *a.* carpellary leaf (*bractea* of R. Brown). *b.* placenta (open *ovarium* of R. Brown). *c.* nucleus. *d.* commencing integument (*cupula* auct.). *e.* embryo-sac. About this time the carpellary leaf has already acquired its green colour, but the *placenta* consists of colourless succulent cellular tissue.

Fig. 19—23. Different periods in the development of *Statice atropurpurea*. Fig. 19, interior of a very young bud. *a.* *a.* *stamina*. *b.* carpellary leaves. Fig. 20, the same at a somewhat later period. *a.* four carpellary leaves, still disunited. *b.* commencement of the formation of the ovule. *c.* base of the fifth carpellary leaf which has been cut off. Fig. 21, a recent ovule, in which the first tumefaction for the development of the inner integument is already evident. Fig. 22, longitudinal section of the same at a later period. The inner integument *a.* has already extended itself over the entire nucleus *b.*, whilst the external integument *c.* is scarcely visible. Fig. 23, the same at a later period: *a.* *b.* *c.* as before.

Fig. 24. Longitudinal section of an ovule of *Lathræa squamaria* soon after its impregnation. *a.* *integumentum simplex*. *b.* remains of the nucleus (*membrana nuclei*, R. Brown). *c.* embryo-sac already filled with cells. *d.* pollen-tubes. *e.* embryo. *f.* cæcal cavities of the embryo-sac in the parenchyma of the ovule. *g.* *funiculus*.

Fig. 25. Anther-cells of *Pinus abies* inclosing four pollen-forming cells.

Fig. 26. The same, after absorption of the parent cells: a grain of pollen may be perceived in each.

Fig. 27. The same after they have been immersed in water: two grains of pollen are just about to leave the cells; having burst the parietes.

Fig. 28. A single grain of pollen from the same.

Fig. 29. Two pollen-bearing cells of *Podostemon ceratophyllum*.

Fig. 30. Pollen of *Podostemon ceratophyllum* taken from the stigma, from one of which a pollen-tube already proceeds.



















